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Impacts of environmental change and community ecology on the composition and diversity of the southern African monkey fauna from the Plio-Pleistocene to the present.

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Abstract

The southern African cercopithecid (monkey) fauna has undergone a profound change in composition and diversity since the Plio-Pleistocene, with modern species representing only a small part of the diversity that existed in the past. During the Plio-Pleistocene, eleven cercopithecid species were found in southern Africa, as many as six of which might have been contemporaneous. The move to more open environments, plus dispersal from and to southern Africa, have probably contributed significantly to changes in monkey diversity over the past three million years. Some of the Plio-Pleistocene cercopithecids are likely to have lived in the same ecological communities as hominins. In modern primate communities, niche partitioning is sometimes used as a way to minimise competition for resources. This would have been a plausible way to maintain relatively high species diversity in the Plio-Pleistocene primate fauna of southern Africa. Nonetheless, the presence of hominins in the generalist feeder niche could have affected the behaviour of other primates in their communities, specifically the monkeys that today have an eclectic diet. It is also possible that Plio-Pleistocene hominins influenced community structure and behaviour through predation. In conclusion, environmental changes as well as interaction with hominins each contributed to shaping the community structure that is seen in South African monkeys today, but further work is required to reconstruct in more depth the interactions of the ecological communities to which hominins belonged.

Introduction

The southern African monkey fauna has undergone a profound change in composition and diversity since the Plio-Pleistocene. Only three species of Cercopithecidae, *Chlorocebus aethiops*, *Papio hamadryas* –as the subspecies *P. h. ursinus* - and *Cercopithecus mitis*, are

currently found in South Africa (International Union for Conservation of Nature and Natural Resources 2006), none of which are endemic. Lower species richness is often seen at higher latitudes (Eeley & Foley, 1999), so the relatively small number of living monkey species in South Africa compared to Uganda, for example, where eleven species are found (International Union for Conservation of Nature and Natural Resources 2006), might be expected. However, much greater diversity was evident in the Plio-Pleistocene, with at least eleven species identified from the southern African fossil record, possibly as many as six of these existing contemporaneously (Elton 2007).

Hominins were the other large-bodied primates found in southern Africa during the Plio-Pleistocene, with *Australopithecus africanus* recovered from certain Pliocene sites, including Makapansgat and Sterkfontein Member 4, and *Paranthropus robustus* and *Homo* identified at localities that date from the early Pleistocene, such as Swartkrans. In southern as well as eastern Africa, cercopithecid and hominin fossils are often found associated in time and space, and as a result it has been argued that cercopithecid evolutionary histories and adaptive strategies can be used to contextualise those of hominins (Foley 1993; Elton 2000, 2006). In addition, the ecology of cercopithecids past and present might make them the most suitable primate referents for early hominins (Aiello, et al. 2000; Lee-Thorp, et al. 2003; Codron, et al. 2005; Elton 2006). Bearing such issues in mind, this brief review has two main aims. The first is to assess how South African cercopithecid diversity has changed since the Pliocene, considering palaeobiology and dispersals from and to southern Africa, as well as speciation and extinction events. The second aim is to suggest how the presence of hominins might have influenced southern African cercopithecid communities and niches in the Plio-Pleistocene.

Southern African cercopithecid diversity from the Pliocene to the present

The South African cercopithecid fossil record in the past 3 million years (Ma) is characterised by high species diversity at the beginning of the period followed by a reduction in diversity in the Pleistocene (Table 1), although this reduction was not necessarily gradual (Elton 2007). The patterns observed are also complicated by the estimation of species numbers (Elton 2007; also see Figure 1). Correct taxonomic identification of fossil material lies at the heart of discussions of past diversity, and there is ongoing debate about the recognition and validity of some Plio-Pleistocene cercopithecid species from southern Africa. *P. h. robinsoni* has been identified from various southern African sites, including Sterkfontein Member 4 (Delson 1984), but its presence at Sterkfontein Member 4 has been questioned (McKee 1993). In addition to this, there is an ongoing debate about how many *Parapapio* species there were, which would also affect the estimation of diversity at Sterkfontein Member 4, as well as at other sites such as the Makapan Valley Limeworks. Although many workers accept four

species of *Parapapio* in southern Africa (*Pp. jonesi, Pp. broomi, Pp. whitei* and *Pp. antiquus*), it has been argued that the range of size variation found in a combined sample of *Pp. jonesi* and *Pp. broomi* specimens from Sterkfontein could be contained in a single, sexually-dimorphic species (Thackeray & Myer 2004). However, recent work on guenon skull morphology in species with very similar mean body masses has indicated that it is often subtle morphological differences that reflect species boundaries in closely-related monkeys (Cardini & Elton 2008). Thus, although size was used as a basis for initially assigning cercopithecid specimens to different species of *Parapapio*, more sophisticated shape analysis, now used routinely in palaeontology, might benefit our understanding of the taxonomy of the genus.

One of the main drivers of the *Parapapio* multiple species debate is the question over whether three congeners could live in close proximity. Brain (1981:152), for example, commented that it appeared 'remarkable' to find three synchronous species of *Parapapio* at Sterkfontein and other sites in southern Africa. However, arboreal guenons in Africa often aggregate in multi-species groups that offer access to resources (Cords 1987) and protection from predation (Gautier-Hion 1988). These two factors, as discussed below, would have exerted significant pressures on southern African cercopithecids. To mitigate the effects of multiple sympatric species, modern cercopithecids often adjust their behaviours, for example by having larger home ranges (Waser 1987). This would have been a mechanism available to Plio-Pleistocene cercopithecids. Some *Parapapio* species seem to have had distinct adaptive strategies, with dietary and locomotor differences observed between specimens likely to belong to the contemporaneous species *Pp. jonesi* and *Pp. broomi* (Elton 2001; Codron, et al. 2005; El-Zaatari, et al. 2005). If this was the case, sympatry, if it occurred, would also have been possible, with alternative modern cercopithecid models being sympatric Asian macaques: *Macaca fascicularis* and *M. nemestrina* are just one example of sympatric congeners that show significant differences in locomotion and habitat use. Thus, given the need for further morphological study of *Parapapio* to investigate its taxonomy, plus observations on modern cercopithecids that demonstrate that sympatry between several species of the same genus is possible, it will be assumed in this review that the four recognised species of *Parapapio* were present in Plio-Pleistocene southern Africa, some of which may have coexisted in the same ecosystem.

During the Plio-Pleistocene there was considerable species turnover in southern African monkeys. *Parapapio*, speciose in Pliocene deposits in southern Africa, had largely disappeared by the early Pleistocene. The genus *Theropithecus*, found at Makapansgat, Swartkrans and Sterkfontein Member 5, but not in the intermediate Sterkfontein Member 4 fauna, was represented by two species, *T. darti* at Makapansgat and *T. oswaldi* at the other sites. At or shortly after 1.75 Ma, there was a radiation of large terrestrial papionins (baboon-

like monkeys), with *Dinopithecus ingens* and *Gorgopithecus major*, which were likely to have originated in southern Africa, joining the two *Papio* species (also probably a southern African native) and the terrestrial colobine *Cercopithecoides williamsi* in the cercopithecid fauna. However, by around or just after 1.0 Ma, the number of cercopithecid species in southern Africa had declined markedly. *T. oswaldi* and *P. h. robinsoni* were the only monkeys recovered from the Swartkrans Member 3 faunal assemblage. *T. oswaldi* is also found at the later site of Hopefield, dated to around 0.7 - 0.4 Ma (Klein & Cruz-Uribe 1991); this occurrence might represent either a 'residual' population from the original *T. oswaldi* colonisation of southern Africa or a 'third wave' of *Theropithecus* movement into southern Africa (Pickford 1993).

The turnover observed prior to 1.0 Ma was due in part to regional environmental change (Elton 2007). Palaeoecological reconstructions indicate wooded, relatively closed environments at Makapansgat (Sponheimer et al. 1999; Sponheimer & Lee-Thorp 2003) and Sterkfontein Member 4 (Bamford 1999), with southern African environments becoming more open after 2 Ma (Watson 1993; Avery 1995; Reed 1997; Luyt & Lee-Thorp 2003). Palaeobiological studies of Plio-Pleistocene monkeys from southern Africa indicate the presence of a range of adaptive strategies, at least in the Pliocene. Ecomorphic analysis of postcranial elements sampled from Makapansgat, Sterkfontein Member 4 and Bolt's Farm suggests that cercopithecids from these sites exploited grassland, bushland/open woodland and forest environments, with some species using arboreal locomotion and others using predominantly terrestrial locomotion (Elton, 2000; 2001). In contrast, the cercopithecid assemblages from the more recent sites of Kromdraai and Swartkrans are dominated by species that apparently preferred terrestrial locomotion in more open habitats (Elton, 2000; 2001). Direct dietary evidence, from tooth microwear (El-Zaatari, et al., 2005) and stable carbon isotopes (Codron et al. 2005), also indicates that there was significant inter- and intraspecific variation in the dietary strategies of southern African cercopithecids during the Plio-Pleistocene. One of the most striking results is the ability of these monkeys to use C_4 resources (tropical grasses) in their diets (Codron, et al., 2005). This, plus the shift in locomotor strategies and habitat preferences through time, suggests that the evolution of the cercopithecid community in this region was closely tied to the expansion of more open habitats (Elton, 2001, 2007; Codron et al. 2005).

In addition to species turnover, dispersals from other parts of Africa contributed to southern African cercopithecid diversity in the Plio-Pleistocene. Such dispersals were not confined to monkeys: faunal exchange between southern and eastern Africa occurred in a number of mammalian groups, including hominins, during this period (Turner & Wood 1993; Strait & Wood 1999; Foley 1999). The major cercopithecid interchanges were the expansion of *T. darti* and *T. oswaldi* from eastern to southern Africa, probably in two waves (Pickford

1993; Hughes et al. 2008), movement of *Cercopithecoides williamsi*, possibly out of eastern Africa (Benefit 1999), and the dispersals of *Parapapio* and *Papio* from southern Africa (Benefit 1999). Nonetheless, two essentially different cercopithecid communities existed in these continental regions during the Plio-Pleistocene: eastern and southern Africa remained the strongholds for *Theropithecus* and *Parapapio* / *Papio* respectively, and the large colobines were consistently more abundant and speciose in East Africa (Benefit 1999).

Notwithstanding dispersals into southern Africa during the Plio-Pleistocene, by the Middle Pleistocene cercopithecid diversity appeared to reduce dramatically, with *P. hamadryas* being the only Plio-Pleistocene species to survive to the present day in South Africa. The modern southern African subspecies *P. h. ursinus* is co-occurs with another modern species, *C. aethiops*, in the fossil record from the Late Pleistocene. Both are found at Border Cave (Klein 1977), and *Cercopithecus* (probably more accurately designated as *Chlorocebus*) and *Papio* have been identified from Black Earth Cave (Peabody 1954). At least seven more Pleistocene / Middle Stone Age sites including Swartkrans Member 5 have yielded *P. h. ursinus*, some in association with *H. sapiens* (Peabody 1954; Humphreys 1974; Klein 1979; Singer & Wymer 1982; Grine & Klein 1991, 1993; Klein et al. 1991; Brain 1993). *P. h. ursinus* probably evolved in southern Africa (Newman et al. 2004) whereas *C. aethiops*, found in the Middle Pleistocene record of Ethiopia (Alemseged & Geraads 2000) and able to disperse widely in the increasingly open environments of Pleistocene Africa, was very probably a Middle to Late Pleistocene immigrant (Elton 2007). There is no obvious fossil record for the third species, *Cercopithecus mitis*, which probably radiated in the late Quaternary, with the current distribution in South Africa dating to after the last glacial maximum (Lawes 1990, 2002).

Today, the three monkey species found in South Africa are all relatively ecologically flexible, and are widespread in sub Saharan Africa. *C. mitis*, although being dependent on forest habitats and found mainly in the far east of South Africa (Lawes 1990, 2002), is often regarded as one of the most ecologically flexible arboreal guenons. The most abundant South African monkeys, *P. h. ursinus* (the baboon) and *C. aethiops* (the vervet), are eurytopic. Primarily adapted to open environments, they nonetheless exploit a range of habitats and are distributed widely across South Africa, with *P. h. ursinus* having the greater geographic range. Both species feed eclectically and can exist in environments that are heavily modified by human activity. The ecological and behavioural flexibility that is evident to a greater or lesser extent in all the modern South African cercopithecids could have been key to their survival outside Central African forest refugia in the climatic fluctuations of the Pleistocene. Another key to their success, at least in *P. h. ursinus* and *C. aethiops*, was probably the ability to live alongside humans. Some of the most successful modern non-human primates are those that can adapt to environments modified by humans. Baboons

and vervets are so good at exploiting human environments that they are regarded by many communities as 'pest' species (Fedigan & Fedigan 1988; Hill 2002). Given their association with *H. sapiens* in the fossil record, it is likely that they have been coexisting closely with humans since at least the Late Pleistocene.

Large-bodied primate communities and niches in the Plio-Pleistocene of southern Africa

Close association between monkeys and hominins probably began much earlier than the Late Pleistocene. Cercopithecids are found at most of the major southern African Plio-Pleistocene hominin sites, so it is likely that in some areas monkeys and hominins belonged to the same ecological community, although association in the fossil record is no guarantee of coexistence in either time or space. It is difficult to judge sympatry from the evidence available in the fossil record (Elton 2006), but coexistence of, and interaction between, contemporaneous hominins and cercopithecids was possible, if not probable. For example, at the East African archaeological site of Olorgesailie, butchery marks on *Theropithecus oswaldi* bones (Shipman et al. 1981) indicate sympatry between at least one hominin and one monkey species during the Pleistocene. In areas of high species diversity, modern African primate communities often contain representatives of several primate radiations, including apes, monkeys and strepsirhines (Reed & Bidner 2004). There is no reason to suppose that similar sympatry could not have occurred in southern Africa during the Plio-Pleistocene.

Organisms that form part of the same ecological community can have a profound impact on one another, influencing feeding behaviour, group structure and habitat use. Having access to resources is fundamental to survival and reproduction, so consideration of diet and feeding behaviour is essential when exploring the possible relationships within past communities. Plio-Pleistocene hominins were probably generalist feeders, exploiting C_3 and C_4 foods (Wood & Strait, 2004; Peters & Vogel, 2005). Dietary components might have included vertebrates, invertebrates, fruits and tubers (Sponheimer & Lee-Thorp, 1999; Backwell & d'Errico, 2001; Lee-Thorp, et al., 2003; Wood & Strait, 2004; Plummer, 2004; Peters & Vogel, 2005). Several modern cercopithecid species also forage eclectically, and dental microwear indicates that at least one Plio-Pleistocene papionin from southern Africa, *Dinopithecus ingens*, had a very varied diet (El-Zaatari, et al., 2005). In addition, recent stable carbon isotope evidence indicates that, like hominins, many Plio-Pleistocene cercopithecids from southern Africa exploited C_4 foods to a greater or lesser extent (Codron, et al., 2005). Competition for resources within large-bodied primate communities, and within the faunal community as a whole, could therefore have been a very real possibility. In an extreme form, this might have led to competitive exclusion of one or more species. Niche

partitioning, whereby coexistence is facilitated through altering the way or frequency in which resources are used, might have been an alternative solution, and a way in which southern African primates might have avoided competition for identical resources. This approach is certainly used in modern African primate communities (for example, guenons: Buzzard, 2006), and probably helps to maintain species diversity.

There is some evidence for niche partitioning in Plio-Pleistocene southern African monkeys. At Makapansgat, for example, the diets of *Pp. jonesi* and *Pp. broomi* were probably quite different, with *Pp. jonesi* being a grass or leaf-eater and *Pp. broomi* preferring fruit (El-Zaatari et al. 2005). Assuming sympatry, the four large terrestrial cercopithecids at Swartkrans, *P. h. robinsoni*, *Cercopithecoides williamsi*, *D. ingens* and *Theropithecus oswaldi*, may have reduced competition through altering the frequencies in which certain resources were used. *P. h. robinsoni* and D. ingens, primarily C_3 consumers (Codron, et al., 2005), could have partitioned resources through differential consumption of fruit and leaves, with *P. h. robinsoni* being more folivorous and *D. ingens* more frugivorous (El-Zaatari et al. 2005). *C. williamsi* and *T. oswaldi* both appear to have included substantial proportions of C_4 foods in their diets, although the *C. williamsi* data suggest highly variable consumption of tropical grass-based resources (Codron et al. 2005). Dental microwear indicates that whereas *C. williamsi* was primarily a leaf or grass-eater, *T. oswaldi* had a reasonably varied diet, possibly consuming some fruit in addition to grass and/or leaves (El-Zaatari, et al., 2005). These interpretations largely fit with observations based on gross molar morphology (Benefit 1999), and are also consistent with stable carbon isotope analyses that indicate that some C_3 foods were incorporated into the diets of both *C. williamsi* and *T. oswaldi* (Codron, et al., 2005). The *T. oswaldi* findings from southern Africa also fit with microwear data from eastern Africa, that point to a greater degree of variability in the diet of *T. oswaldi* compared to that of the one modern species, *T. gelada* (Teaford 1993), supporting assertions that the ecology of *T. gelada* is not analogous to those of the extinct *Theropithecus* species (Elton 2000, 2002; Codron et al. 2005). Thus, by varying the proportions of different plant types in the diet and using different plant parts, it is not implausible that the four large terrestrial cercopithecids at Swartkrans could have been sympatric whilst avoiding direct competition.

What, then, were the likely roles of hominins in southern African primate communities? In eastern Africa, although the palaeobiologies of Plio-Pleistocene primates are not as well studied as those in southern Africa, it is possible that hominins filled the generalist dietary niche to the exclusion of monkey generalists (Elton 2006). However, there are differences between the hominin fauna of eastern and southern Africa. As many as four contemporaneous hominin species have been recorded in parts of East Africa, such as the Upper Burgi and KBS members at Koobi Fora (Turner et al., 1999). In southern Africa, the maximum apparent number of synchronous species was two, for example at Swartkrans (de

Ruiter 2003). Due to this, cercopithecids might have faced less competition from hominins in southern Africa than in eastern Africa, allowing certain species, such as *D. ingens*, to radiate into terrestrial niches and exploit a wide range of dietary resources. Nonetheless, on current evidence, few monkey species at southern African Plio-Pleistocene sites appear to have been highly generalist, although they might have been very flexible in their feeding behaviours. One very interesting finding to emerge from recent dietary work is that *P. h. robinsoni* at Swartkrans was more folivorous than suggested by previous studies (El-Zaatari et al. 2005). Observations on modern *P. hamadryas* subspecies demonstrate an impressive amount of dietary diversity, including numerous plant species, insects, eggs and birds (Altman 1998), but in times of food scarcity, many baboon populations exploit increased quantities of 'fallback' items such as grass corms (Alberts, et al., 2005). This is observed today under seasonal regimes (Alberts, et al., 2005), but could also have been a strategy used by extinct baboons in the face of competition from other animals, including hominins.

Modern humans undoubtedly influence the primate communities around them in a variety of ways, including providing access to cultivated foods such as crops, through hunting, and by encroaching on habitats because of settlement or logging. Thus, competition for resources apart, the presence of Plio-Pleistocene hominins might have affected primate communities. The most obvious way by which this could have occurred was through hunting. There is good evidence for hominin predation on large monkeys in eastern Africa (Shipman et al. 1981), and evidence for hominin modification of ungulate bone has been found in southern Africa, such as at Swartkrans Member 3 (Pickering et al., 2004). Analogy with modern chimpanzees suggests that hominins may have hunted other primates, and this could well have affected cercopithecid populations; at Gombe National Park (Tanzania), for example, chimpanzee predation pressure has a significant limiting effect on group size in red colobus monkeys (Stanford 1995). Thus, although much work remains to be done on hominin predation of monkeys in Plio-Pleistocene southern Africa, the possibility that hominins were not only cercopithecid competitors but also predators, helping to shape group structures and behaviour patterns, cannot be dismissed.

Summary and conclusions

The modern cercopithecid fauna of South Africa represents only a small part of the diversity that existed in the past. Environmental changes, including the move to more open habitats in southern Africa (Elton 2007) as well as interaction with hominins, the other large-bodied primates to be found in southern Africa, both contributed to shaping the community structure that is seen in monkeys today. Attention must now be paid to examining in more detail the evolutionary histories, taxonomies and palaeobiologies of Plio-Pleistocene monkeys in southern Africa and elsewhere, in order to build more robust models of community ecology

and help reconstruct the interactions of the ecological communities to which hominins belonged.

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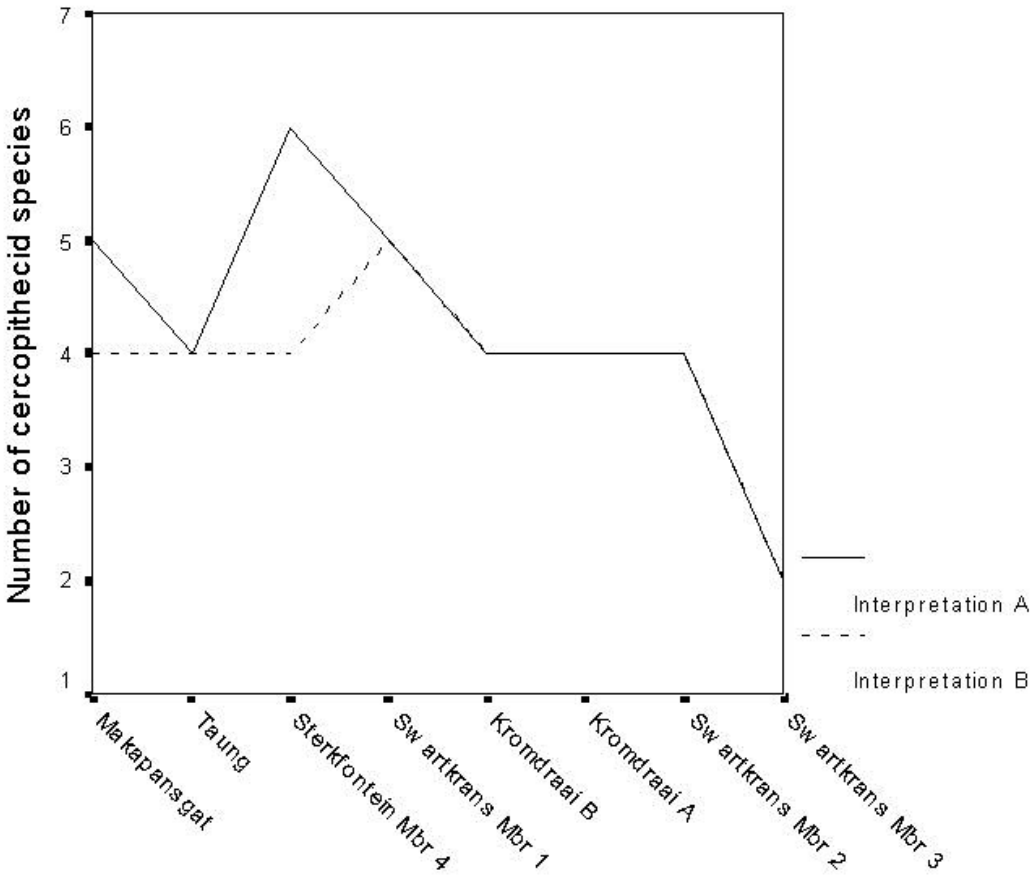

Figure 1: Cercopithecid species counts at some major southern African Plio-Pleistocene palaeoanthropological sites. Primary data are taken from the Paleobiology Database, supplemented as listed in Table 1. Sites are shown in chronological order from earliest to most recent. Interpretation A uses a traditional estimate of species numbers at these sites, Interpretation B a more conservative estimate in which specimens assigned to *Pp. broomi* and *Pp. jonesi* are treated as conspecific (after Thackeray & Myer, 2004) and *P. h. robinsoni* is not recognised at Sterkfontein Mbr 4 (McKee, 1993). The significant reduction in species count over time is evident. In the mid or late Pleistocene, *P. hamadryas* (as the subspecies *P. h. ursinus*) was joined by two guenon species that dispersed into southern Africa, *C. aethiops* and *C. mitis* (not shown).

Table 1: Primate species occurrences at some major southern African Plio-Pleistocene palaeoanthropological sites. Sites are listed in chronological order from left to right. Data are taken from the Paleobiology Database, based on Vrba (1975), Butler & Greenwood (1976), Brain (1976, 1981, 1994), Partridge (1978, 1982), Jones, Brock & McFadden (1986). Supplemented by Delson (1984), Turner et al. (1999), Elton (2001), Jablonski (2002), de Ruiter (2003).

	Makapansgat	Taung	Sterkfontein Member 4	Swartkrans Member 1	Kromdraai B	Kromdraai A	Swartkrans Member 2	Swartkrans Member 3
T. darti	+							
Pp. whitei	+	+	+					
Pp. broomi	+		+					
Pp. jonesi	+	+	+	+		+		
C. williamsi	+		+	+	+		+	
Pp. antiquus		+						
P. izodi		+	+		+	+		
P. h. robinsoni			+	+	+	+	+	+
T. oswaldi				+			+	+
D. ingens				+			+	
G. major					+	+		
A. africanus	+	+	+					
P. robustus				+	+		+	+
***Homo* sp.**				+			+	